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New Taxa of Brachynomadine Bees
(Apidae: Nomadinae)

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CONTENTS

Abstract	2
Introduction	2
Acknowledgments	2
Morphology	3
Key to Genera and Subgenera of Brachynomadini	3
<i>Kelita</i> Sandhouse	5
<i>Spinokelita</i> , new subgenus	5
<i>Kelita</i> (<i>Spinokelita</i>) <i>argentina</i> , new species	5
<i>Brachynomada</i> Holmberg	9
<i>Brachynomada</i> (<i>Brachynomada</i>) <i>scotti</i> , new species	9
Adult	9
Pupa	13
Larva	14
Biological Notes on <i>Brachynomada scotti</i> and Its Host, <i>Exomalopsis bruesi</i>	15
Observations	15
Discussion	17
<i>Triopasites</i> Linsley	19
<i>Triopasites penniger</i> (Cockerell)	20
<i>Triopasites spinifera</i> , new species	22
Phylogenetic Considerations	24
References	25

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ABSTRACT

The following new taxa of cleptoparasitic bees belonging to the Brachynomadini are described: *Spinokelita*, new subgenus of *Kelita*, type species *Kelita (Spinokelita) argentina*, new species, from Argentina; *Brachynomada (Brachynomada) scotti*, new species, from Peru; and *Triopasites spinifera*, new species, from Mexico. A key based on adult characters is presented for the genera and subgenera of the Brachynomadini.

The pupa and larva of *Brachynomada scotti* are described taxonomically, and the biology of *B. scotti* and its ground-nesting host, *Exomalopsis (Exomalopsis) bruesi* Cockerell, is detailed. Several new characters involving male terminalia distinguish the subgenera *Brachynomada* and *Melanomada*. A table lists species of Exomalopsini with their known nomadine cleptoparasites. *Brachy-*

nomada (B.) scotti is the first species in the nominate subgenus reported to attack nests of *Exomalopsis*, and *E. (E.) bruesi* is the first member of its nominate subgenus reported to host a brachynomadine.

A review of *Triopasites* places the following species in synonymy with *T. penniger* (Cockerell, 1894): *pasitura* (Cockerell, 1935); *timberlakei* Linsley, 1939; *micheneri* Linsley, 1943; and *laguna* Linsley, 1943, ALL NEW SYNONYMY. The description of *Triopasites spinifera* and synonymy of all others results in a recharacterization of *Triopasites*.

The tribe appears to be divided into two main clades, one consisting of *Brachynomada* (including *Melanomada*), *Paranomada*, *Triopasites*, and *Trichonomada* and the other consisting of *Kelita* with its new subgenus *Spinokelita*.

INTRODUCTION

Brachynomadini is a recently named New World tribe of cleptoparasitic bees (Roig-Alsina and Michener, 1993), the systematics of which is still in flux because of the rarity of collections. Michener (1996) recently identified a new brachynomadine genus (*Trichonomada*), synonymized some of the taxa included in the tribe, and characterized the currently recognized genera. The present paper furthers our understanding of the anatomical diversity, host preferences, and geographic range of the tribe by describing a new subgenus and species of *Kelita* and a new species of *Brachynomada* from Peru and by revising *Triopasites*, including recognizing a new species from Mexico.

This paper does not discuss the monophyly of the tribe, which was established by Roig-Alsina and Michener (1993) and examined further by Rozen (1996) and Rozen et al. (1997).

ACKNOWLEDGMENTS

Fieldwork in Peru leading to the collection and study of *Brachynomada scotti* was kindly supported by Robert E. Goelet, Chairman Emeritus, American Museum of Natural History. Gerardo Lamas Mueller, Museo de Historia Natural, Lima, Peru, greatly facilitated the collecting trip. The National Geographic Society (grant 3844-88) funded the expedi-

tion to Argentina on which the holotype of *Kelita argentina* was obtained. Most of the specimens of *Triopasites spinifera* were collected under the aegis of the Programa Cooperativo Sobre la Apifauna Mexicana (PCAM), supported by a National Science Foundation grant (BSR 90-24723) to the University of Illinois (W. E. LaBerge, principal investigator).

I acknowledge with appreciation the field assistance and friendly companionship of the late Luis E. Peña and Alfredo Ugarte on the trip to Argentina and of Alfredo Ugarte on the trip to Peru.

Fernando A. Silveira kindly identified *Exomalopsis bruesi* Cockerell; Zachary Falin tentatively identified *Macrosiagon vittatum* (Erichson).

Specimens used in this study were made available from the following collections: Bee Biology and Systematics Laboratory, Utah State University, Logan (G. E. Bohart, T. Griswold); California Academy of Sciences, San Francisco (W. Pulawski, D. Ubick); Central Texas Melittological Institute (J. L. Neff); Essig Museum of Entomology, University of California, Berkeley (C. B. Barr); Natural History Museum of Los Angeles County, California (R. R. Snelling); Programa Cooperativo sobre la Apifauna Mexicana (PCAM), University of Illinois, Champaign

(W. E. LaBerge, D. Yanega); Snow Entomological Division, Natural History Museum, University of Kansas, Lawrence (R. W. Brooks, C. D. Michener).

Light micrographs were taken by David A. Grimaldi, and SEM micrographs were made by Peling Fong-Melville.

I thank the following persons for their helpful comments on the manuscript: Drs. Bryan N. Danforth, Cornell University; Charles D. Michener, University of Kansas; and Arturo Roig-Alsina, Museo de Ciencias Naturales, Buenos Aires, Argentina.

MORPHOLOGY

The tergal and sternal graduli of most brachynomadine genera exhibit an unusual modification.² The gradulus of most segments (but not the first) is produced posteriorly as a thin, nearly transparent lamella, which in figure 21 appears paler than the pregradular area. Because of this transparency, the base of the lamella appears as a dark line (arrow, fig. 21) running transversely across the tergum or sternum and might be misinterpreted as being a ridgelike (nonlamellate) gradulus. However, on close inspection, the thin posterior edge of the gradulus can be detected, with setae arising under the lamella. The outer surface of the lamella is completely continuous with the pregradular area, and on a coated specimen (fig. 22) the dark line of its base is invisible and its posterior edge is quite apparent. The lamellate condition of the gradulus, almost certainly a synapomorphy, is shared by males and females of *Triopasites* (see fig. 28 for diagram of gradular lamellae of T2 and S2 of male of *T. penniger*), *Brachynomada* sensu lato, *Paranomada*, and *Trichonomada*, that is, the brachynomadine lineage in its entirety. This condition is not found in the kelitine lineage (*Kelita* sensu stricto and *Spinokelita*). In the brachynomadine lineage, the posterior edge of the lamella probably rides against the tergum/ster-

num of the preceding metasomal segment. It may function to deflect the stinger of a host female if the host attempts to sting the cleptoparasite between the metasomal segments. Trapped at the sclerotized base of the lamella, the tip of the stinger would be excluded from the soft, easily penetrable, intersegmental membrane.

The sizes and shapes of the lobes and appendages arising from near the apex of the male gonocoxites of members of this tribe show considerable taxonomic diversity. Terminology applied to them has often varied, and intertribal homologies of these structures need to be established. However, within the Brachynomadini, homologies seem clear, and the anatomical terminology of Ehrenfeld and Rozen (1977) and Rozen (1994) is adopted here because it provides names for most of the taxonomically important structures.

The following abbreviations are used: T = metasomal tergum; S = metasomal sternum. Hence, S7 refers to the seventh metasomal sternum, etc. In descriptions, the *eye-convergence index* is the lower interocular distance divided by the upper interocular distance. In the illustrations, anterior ends of anatomical parts are oriented either toward the top of page or to the left.

KEY TO GENERA AND SUBGENERA OF BRACHYNOMADINI

The following key, revised in part from Michener (1996), is presented because of the recognition of a new subgenus of *Kelita* and a drastic change in the generic concept of *Triopasites*. The latter was brought about by synonymies of included species and recognition of a new one from Mexico. This key is provisional, based on described taxa; other species, some already collected but yet to be studied and described, will probably further modify our generic concepts.

1. Hind coxa broadly expanded laterally, with pronounced longitudinal carina along mesal dorsal edge and strong carina along outer dorsal edge, separated by strongly concave, mostly glabrous surface; antennal scape normally long, length exclusive of basal ball distinctly greater than twice maximum diameter; graduli of most anterior terga and sterna (but not T1 and S1) produced as distinct, clear, thin posteri-

² This modification is not as unusual as I had originally thought. After reviewing this manuscript, Dr. Arturo Roig-Alsina (personal commun.) informed me that "lamellate graduli are also found in Exomalopsini, Eucerini, many tapinotaspines, and also in the Isepeolini." He also stated that they are characteristic of emphorines and *Oreopasites* (Nomadinae).

only directed lamellae (not just carinae) that lie close to postgradular areas (figs. 21, 22, 28) 3

Hind coxa normal, not expanded, with carina along mesal dorsal edge but without carina along outer dorsal edge; antennal scape short, length exclusive of basal ball less than twice maximum diameter; graduli of anterior terga and sterna normal, simple ridges. *Kelita* sensu lato 2

- 2(1). Forewing with two submarginal cells; maxillary palpus six-segmented; male hind tibia normal, not broadly expanded apically; male hind tibial spurs normal in size, subequal in length; dorsal and median processes of gonostylus shorter than length of gonocoxite. Chile
 *Kelita* Sandhouse sensu stricto³

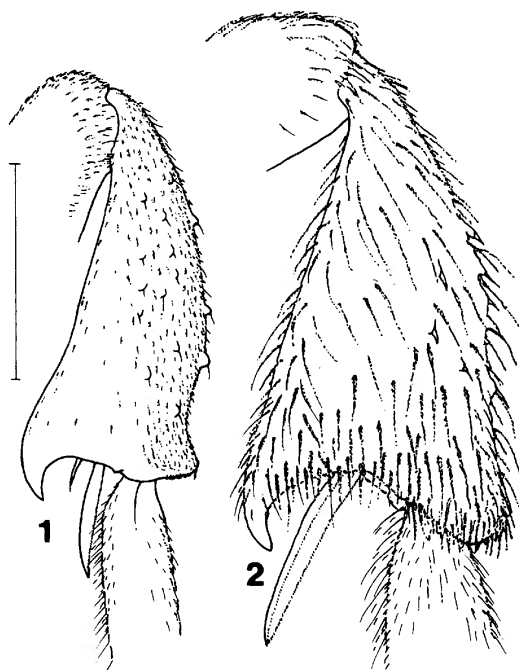
Forewing with three submarginal cells; maxillary palpus five-segmented; male hind tibia broadly expanded apically with anterior edge forming down-curved spine (fig. 1); male with one normal-sized hind tibial spur, second one absent or extremely short; dorsal and median processes of gonostylus (figs. 3, 4) elongate, length distinctly greater than that of gonocoxite. Argentina . . . *Spinokelita*, new subgenus

- 3(1). Anterior mandibular articulation removed from eye by distance almost as great as ocellar diameter 4

Anterior mandibular articulation almost as close to eye as posterior articulation, removed from eye by distance no greater than $\frac{1}{2}$ ocellar diameter 5

- 4(3). Mesosoma not strongly flattened; sparse setae on eyes about half as long as ocellar diameter; frons in front of ocelli punctate, not particularly shiny; scutal disc punctate; maxillary palpus five-segmented (counting minute segment 1); S5 of female broadly rounded apically; clypeus of male with low lateral carina in addition to deep suture immediately above it, extending from anterior tentorial pit to anterior mandibular articulation. Argentina, Brazil *Trichonomada* Michener

Mesosoma strongly flattened; sparse setae of eyes minute, scarcely noticeable; frons in front of ocelli nearly glabrous, polished; scutal disc virtually glabrous, highly polished; maxillary palpus usually four-seg-



Figs. 1, 2. Hind tibiae of males of 1. *Kelita* (*Spinokelita*) *argentina* and 2. *Brachynomada* (*Brachynomada*) *scotti*, showing similar modification of apices. Scale (=0.5 mm) refers to both figures.

mented (counting minute segment 1); S5 of female with apical margin produced as round, median projection; male without lateral clypeal carina but with very deep suture (presumably lateral segment of epistomal suture) extending from anterior tentorial pit to anterior mandibular articulation.⁴ Southwestern United States, Mexico⁵ . . .
 *Paranomada* Linsley and Michener

⁴ Linsley and Michener (1937) stated that the holotype of *Paranomada nitida* Linsley and Michener (Phoenix, Arizona) had a five-segmented maxillary palpus. Because specimens of this species from southern Arizona in the collection of the American Museum of Natural History have only four-segmented palpi (including minute segment 1), I borrowed the holotype from the California Academy of Sciences to reexamine this character. Although the right maxillary palpus appeared to have five segments, close inspection showed that this was an artifact resulting from foreign material attached to the terminal segment. Both the right and left palpi are four-segmented, like those of other North American *Paranomada*.

⁵ Although Michener (1996) assigned an unnamed South American species (? = *thoracica* [Friese]) to this genus, he (personal commun.) now believes that it is not a *Paranomada*. I have not seen specimens of that species.

³ Specimens of a small, undescribed species from Argentina with two submarginal cells on the forewing seem to be close to *Kelita* sensu stricto, but their antennal scape is normally long, in contrast to the short scape of the Chilean species of that genus.

- 5(3). Median apical triangle of S1 projecting downward; lateral edges of triangle directed posteriorly as pronounced lamellate carina; males with dorsal process of gonostylus short, laterally flat, wide, and bladelike near base, tapering evenly toward apex as seen in lateral view (figs. 30, 37, 41). Southwestern United States, Mexico. *Triopasites* Linsley
- Median apical triangle of S1 scarcely produced; sides of triangle a simple rounded ridge or weakly carinate, never produced posteriorly as lamella; males with dorsal process of gonostylus (fig. 15) short or attenuate, but slender, sometimes widening near apex, never laterally flat and bladelike. *Brachynomada* sensu lato 6
- 6(5). Males with hind femur normal, without basal thornlike projection or other modification; male with S8 (figs. 17, 18) elongate, strongly produced posteriorly, its apex broadening before ending abruptly. South America
- . . . *Brachynomada* Holmberg sensu stricto
- Male with hind femur (Rozen, 1994: fig. 30) bearing basal thornlike projection ventrally and, in some species, other modification on ventral surface; male with S8 (ibid.: fig. 28) less elongate, not strongly produced, tapering to apex. Western United States, Mexico.
- *Melanomada* Cockerell

KELITA SANDHOUSE

Spinokelita, new subgenus

TYPE SPECIES: *Kelita* (*Spinokelita*) *argentina* Rozen.

DIAGNOSIS: The key and the diagnosis of *Kelita* (*Spinokelita*) *argentina*, below, will separate this subgenus from *Kelita* sensu stricto.

DESCRIPTION: Characters in italics in the following species description are those that differentiate *Spinokelita* from *Kelita* sensu stricto. Characters in boldface support the inclusion of *Spinokelita* in *Kelita* sensu lato.

ETYMOLOGY: *Spino-* refers to the spinelike expansion of the inner apex of the male hind tibia; *-kelita* is the name of the genus.

Kelita (*Spinokelita*) *argentina*,
new species

Figures 1, 3–13

The specimens dealt with here are not certainly conspecific as judged by their anatom-

ical diversity and separation of collection localities. The description of the male is based on the holotype; deviations for other males are noted parenthetically. The description of the female is based on the single available specimen.

DIAGNOSIS: Males and females of this species can immediately be distinguished from those of *Kelita* sensu stricto by their three submarginal cells and five-segmented maxillary palpi. In addition, males bear apically modified hind tibiae (fig. 1) and distinctive genitalia (figs. 3–5).

DESCRIPTION: **Male.** Structure. Head width (maximum distance between outer eye margins) 1.3 times length (vertex to lower margin of clypeus) (1.3–1.5); width 1.8 mm (1.5–1.8 mm); length 1.3 mm (1.0–1.4 mm); wing length 3.7 mm (3.0–3.5 mm); body length 5.0 mm (4.8–5.8 mm).

Vertex not strongly vaulted, so median ocellus touching upper orbital tangent in facial view. Inner orbits converging below; eye-convergence index 0.81. Clypeus with lateral carina evident but perhaps not as pronounced as in *Kelita* s.s.; clypeal disc, supra-clypeal area, and interantennal area somewhat produced; labral disc slightly convex at base, hidden apically on holotype, but faintly concave apically on other specimens; apical margin of labrum hidden on holotype but with one or more median denticles on other specimens. Anterior mandibular articulation almost as close to eye as posterior articulation. Paraocular carina absent. Gena moderately narrow, its maximum width in lateral view about 0.6 times maximum eye width measured at right angles to posterior eye margin (in *Kelita* s.s., gena tending to be broader, ranging from 0.6 to 0.9 times maximum eye width). **Antennal scape short and abruptly narrower at base, as in *Kelita* s.s., not much flattened, length about twice maximum diameter and about half distance from antennal socket to level of median ocellus in frontal view.** Mandible tapering to simple apex, inner dorsal edge with small, obtuse, pointed, inner projection arising from upper margin about 2/3 way to apex. *Maxillary palpus five-segmented*, about 1/2 length of galeal blade; segment 2 longest; segments 3 and 4, each 2/3 length of segment 2; segment 5 slightly shorter than segment 3

or 4; segment 1 of labial palpus somewhat more than 2 times as long as segment 2 (in at least two other specimens, segment 1 less than 2 times length of segment 2).

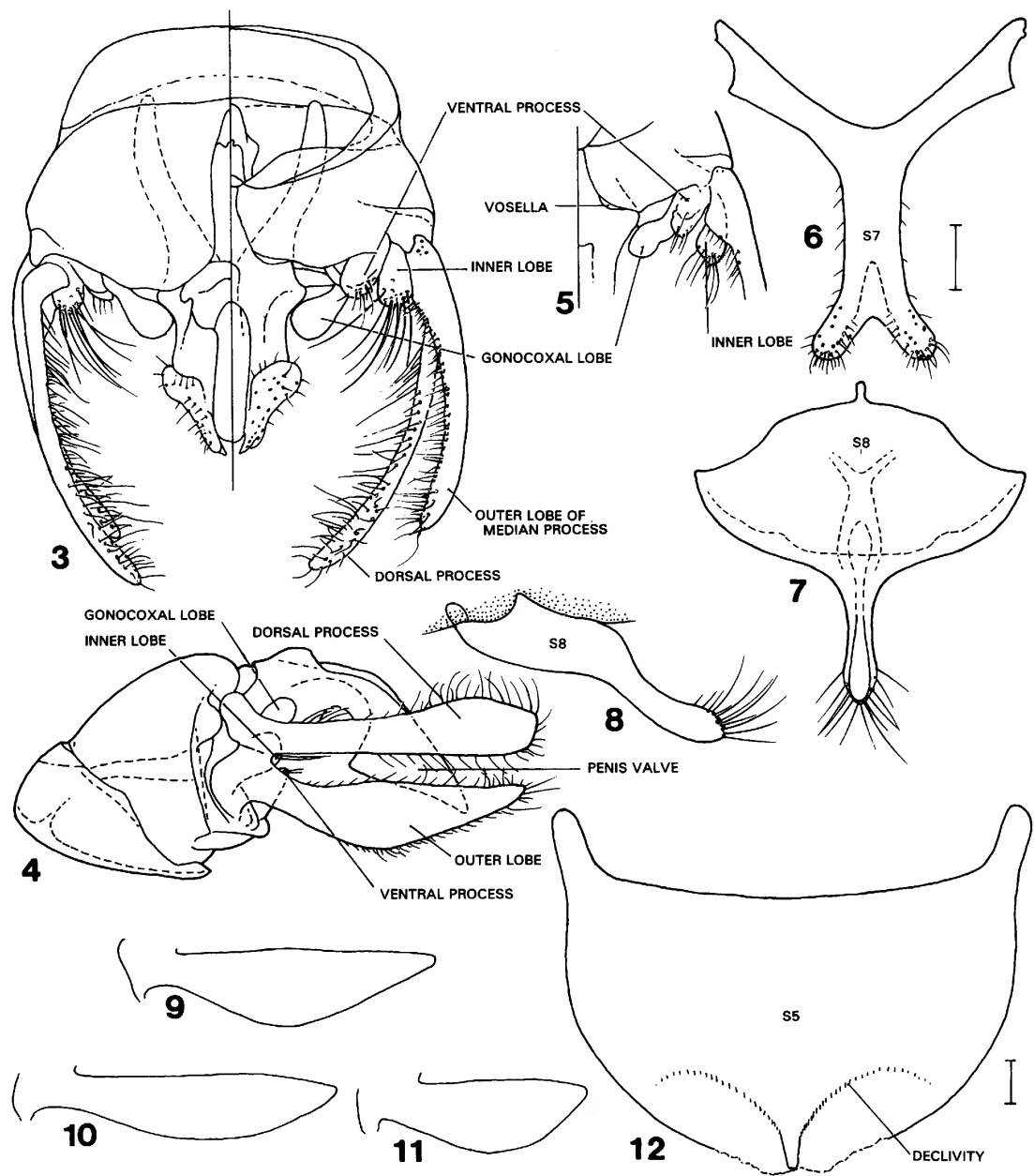
Propleuron normal, without prominent ventrolateral tubercle. Mesoscutum with median line only slightly impressed, highly plumose, appressed setae tending to accentuate appearance of deeper line; parapsidal lines not impressed; mesepisternal scrobe only moderately depressed. *Forewing with three submarginal cells*; apex of marginal cell pointed, slightly removed from wing margin (by about one vein width). Forebasitarsus linear, unmodified but with ventral apical brush of long setae extending as far as apex of second segment. **Hind coxa not expanded laterally as in brachynomadine lineage, with short longitudinal carina at base along mesal dorsal edge and with rounded longitudinal ridge but without carina along outer dorsal edge.** Hind femur normal, without ventral thornlike basal projection; outer apex of hind tibia ending in curved, faintly flared ridge, without projecting point at anterior end; *inner apex of hind tibia (fig. 1) very broad, produced into long curved spine, similar to, though not as broad as, tibial apex of Triopasites spinifera; posterior (inner) hind tibial spur normally long and robust, but anterior (outer) spur greatly reduced, less than $\frac{1}{3}$ length and diameter of inner spur* (in three other specimens, outer spur entirely absent; in one other specimen, one tibia with single normal spur, other leg with single spur $\frac{1}{3}$ length of normal spur).

Graduli of anterior terga and sterna ridges or fine carinae, but not produced as distinct, clear, thin posteriorly directed lamellae as is characteristic of brachynomadine lineage (see Morphology, above). Pygidial plate (T7) apically rounded (on one other specimen, faintly notched medially). Median apical triangle of metasomal S1 not produced, sides of triangle faint rounded elevations; surface of triangle with recumbent plumose setae only. *S7 (fig. 6) with apical process more elongate than in Kelita s.s., flaring apically in ventral view, and with apex more deeply bifurcate than in Kelita s.s.; S8 (figs. 7, 8) with median process slender, fingerlike, as in Kelita s.s., but more elongate; basal plate broader than in Kelita*

s.s. Gonocoxites (figs. 3, 4) very broad relative to length and height, in contrast to those of Kelita s.s.; dorsal process and outer lobe of median processes of gonostylus extremely elongate, longer than gonocoxite and longer than those of Kelita s.s.; broadest part of outer lobe of median process in lateral view less than halfway to apex (in two other specimens (figs. 10, 11), broadest part more than halfway to apex); inner lobe of median process (fig. 3) distinct, projecting in dorsal and ventral views about as far as ventral process but not as far as gonocoxal lobe (in one other specimen (fig. 5), inner lobe more elongate, projecting beyond ventral lobe about as far as gonocoxal lobe); setae of inner lobe tending to be longer and stouter than those of outer lobe and dorsal process; setae of ventral process tending to be shorter than those of dorsal and median processes.

Color. Head, mesosoma, and metasoma very dark brown to black, except lateral pronotal lobes, tegulae, and legs tending to be vaguely ferruginous (in some specimens, labrum and scape also paler). Anterior wing tips faintly infuscated; wing veins and stigma blackish brown.

Integumental texture and vestiture. Compound eyes with scattered minute hairs (also present in some *Kelita* s.s.). Integument of vertex, frons, and clypeus densely punctate, with punctures moderately fine, generally contiguous (except in vicinity of lateral ocelli), interspaces shiny; vertex partly obscured by short, recumbent, coppery, plumose pubescence, which becomes white near eyes; clypeus, upper paraocular, and supraclypeal areas with even denser, more strongly plumose, short, white pubescence that nearly obscures integument (in some specimens, this pubescence worn); lower paraocular area between clypeal carina and eye shiny, nearly impunctate, similar to that of *Kelita* s.s. (Ehrenfeld and Rozen, 1977: fig. 14). Scape and pedicel with short pubescence that only partly obscures integument. Mesoscutum densely, evenly punctate; punctures nearly contiguous, moderately fine; interspaces shiny; mesoscutal pubescence recumbent, very short, coppery on disc except along midline and parapsidal lines, elsewhere whitish. Mesepisternum with integument nearly obscured by short, white, highly plumose, recumbent



Figs. 3–12. *Kelita (Spinokelita) argentina*. 3. Male genitalia of holotype, dorsal (left) and ventral (right) views. 4. Same, lateral view. 5. Part of male genitalia of specimens from 2.8 km east of Los Antiguos, Argentina, showing variation in lengths of ventral process and inner lobe of median process of gonostylus relative to length of gonocoxal lobe, ventral view. 6. S7 of male, ventral view. 7. S8 of male, ventral view. 8. Same, lateral view. 9–11. Outer lobe of median process, in maximum lateral profile, of holotype, of specimen from 13 km north of Puerto Madryn, and of specimen from 2.8 km east of Los Antiguos, respectively, showing variation of shape. 12. Diagram of S5 of female from 13 km north of Puerto Madryn, Argentina, ventral view. Scales (=0.1 mm) refer to figures 3–11 and figure 12 respectively.



Fig. 13. Western South America, showing known distributions of *Kelita* (*Spinokelita*) *argentina* (closed symbols) in Argentina and *Brachynomada* (*Brachynomada*) *scotti* (open symbols) in Peru and Ecuador. Stars indicate type localities.

vestiture. Wings only moderately hairy. Hind coxa with dorsal surface between outer longitudinal ridge and mesal carina shiny, only vaguely sculptured, but with dense patch of

recumbent white setae near base on outer part of surface. T1 with basal patch of very short, recumbent, whitish, plumose setae that partly obscure integument; premarginal area of T2–T5 with transverse band of whitish setae similar to those of T1; marginal areas of T2–T5 laterally with similar setae; all these setae giving metasoma pruinose appearance.

Female. Structure. Head width 1.5 times length; width 1.8 mm; length 1.3 mm; wing length 3.5 mm; body length 5.3 mm.

As described for male, except for following: Inner orbits converging below, with eye-convergence index 0.79. Clypeal carina absent. Paraocular carina short but present. Gena narrow, somewhat less than half width of eye in lateral view, measured at right angles to posterior eye margin. As in holotype, segment 1 of labial palpus more than 2 times length of segment 2.

Forebasitarsus without ventral apical brush. Inner apex of hind tibia not expanded anteriorly as in male; *outer apical angle slightly flared, with small but dense mat of very short setae on outer aspect (contrasting with sharp-edged outer apical rim of hind tibia of Kelita s.s.)*; hind tibial spurs normal in length, with inner one somewhat longer than outer one, but outer one somewhat less robust at base compared with inner one.

Pygidial plate broad at base, apically subtruncate with median emargination; **S5 with seta-bearing basal part set off from mostly glabrous apical paramedian margin by pronounced declivity (fig. 12); basal part with projection extending medially as acute median process; this process reaching apical margin, bearing small tuft of simple, curved setae at apex; S6 with pair of paramedian processes, which are slightly expanded near apices; each process bearing stout setae apically and more slender setae basally, these setae tending to be retrorse; hence, S6 almost identical to that of *Kelita* s.s. (Ehrenfeld and Rozen, 1977: fig. 21).**

Color. As described for holotype, except labrum, antennae, lateral angles and lobes of pronotum, tegulae, and legs more strongly ferruginous; metasoma brownish.

Integumental texture and vestiture. As described for male, except for following: Setae heavily worn on head and mesosoma, so only short, white, densely plumose, recumbent se-

tae remaining; these setae similar to recumbent white setae of male. Metasoma with whitish setae partly worn but presumably comparable to those of male. **Pseudopygidial area** oval, longer than broad, composed, at least in part, of short, thick, posteriorly directed setae (in contrast to genera of brachynomadine lineage, in which setae are long and posterolaterally directed and therefore differentially reflective on each side).

HOLOTYPE: Male: ARGENTINA, San Juan Prov.: 10 km W. Media Agua, X-30-1991 (J. G. Rozen, L. Peña, and A. Ugarte).

OTHER MATERIAL: ARGENTINA, Chubut Prov.: 1 male, 1 female, 13 km N. Puerto Madryn, 120 m, XII-16-1966 (M. Irwin and E. I. Schlinger). Santa Cruz Prov.: 3 males, 2.8 km E. Los Antiguos, 280 m, XI-21-1966, river dune (M. E. Irwin and E. I. Schlinger). The known distribution of this species is plotted in figure 13 (closed circles and closed star).

ETYMOLOGY: The species name refers to the country of origin of the available specimens.

HOST: Unknown.

REMARKS: *Kelita* (*Spinokelita*) *argentina* is perhaps sufficiently distinct to be considered a separate genus, but its affiliation with the kelitine lineage is well supported by the characters in boldface, above.

BRACHYNOMADA HOLMBERG

Michener (1996) in synonymizing *Melanomada* with *Brachynomada* stated that a basal, thornlike projection on the underside of the male hind femur (ibid.: 89) of North American species "might justify separation of *Brachynomada* and *Melanomada* as subgenera." Several characters have come to light strongly supporting such a distinction. In specimens available to me there are consistent differences in S7 and S8 between *Brachynomada* and *Melanomada*. In males of *Melanomada*, the median apical process of S7 is parallel-sided or tapers apically and bears a more-or-less rounded apex (Snelling and Rozen, 1987: figs. 9, 11, 13, 15 [note that these sterna were mislabeled]). The apical process of S8 (ibid.: figs. 8, 10, 12, 14 [also mislabeled]); Rozen, 1994: fig. 29) is

short and gradually tapers posteriorly. In at least some species of *Brachynomada* sensu stricto, the apical process of S7 broadens apically and its apex is emarginate medially (fig. 16; Rozen, 1994: fig. 23). The apical process of S8 (fig. 17; ibid.: figs. 23–25) is elongate, narrow basally, and expanded apically just before ending. The apical process of S7 of *Paranomada* and *Triopasites* (figs. 31, 38) is more or less like that of *Brachynomada* sensu stricto; the apical process of S8 of these genera (figs. 32, 39) tapers like that of *Melanomada* but is more elongate.

Brachynomada (*Brachynomada*) *scotti*, new species

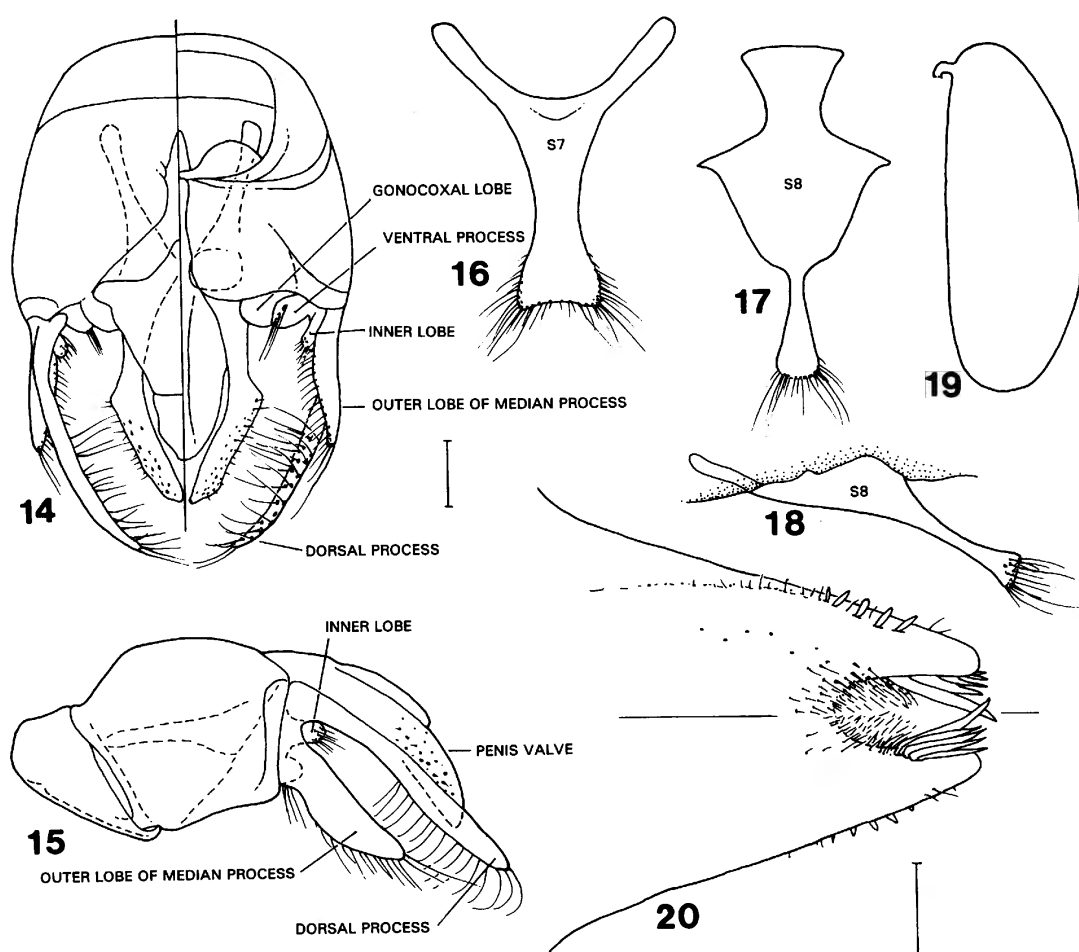
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Figures 13–18, 20

DIAGNOSIS: Males and females of *Brachynomada scotti* differ from those of other species available to me because of their blackish body, fine, dense, even-spaced punctation of the mesoscutum, and somewhat dull aspect of the metasomal terga due to tessellation and fine, dense punctation. Males and females of other species tend to have distinctly reddish areas at least on the base of the metasoma, and their metasomas and mesoscuta are often shiny, more coarsely, less densely punctate. Features by which *Brachynomada scotti* differs pronouncedly from *B. roigi* are italicized below.

DESCRIPTION: Male. Structure. Head width (maximum distance between outer eye margins) 1.3 times length (vertex to lower margin of clypeus); width 1.6–2.0 mm; length 1.2–1.5 mm; wing length 4.0–5.2 mm; body length 5.5–7.5 mm.

Vertex not strongly vaulted, so median ocellus less than one diameter above upper orbital tangent in facial view. Inner orbits converging below; eye-convergence index 0.85. Clypeus with small carina laterally, which is partly hidden by setae; clypeal disc and supraclypeal area slightly convex; *interantennal area not produced* (in *B. roigi*, *area strongly produced along midline*); labral disc flat to faintly concave at base; apical margin of labrum with row of irregular denticles. Anterior mandibular articulation almost as close to eye as posterior articulation. Para-

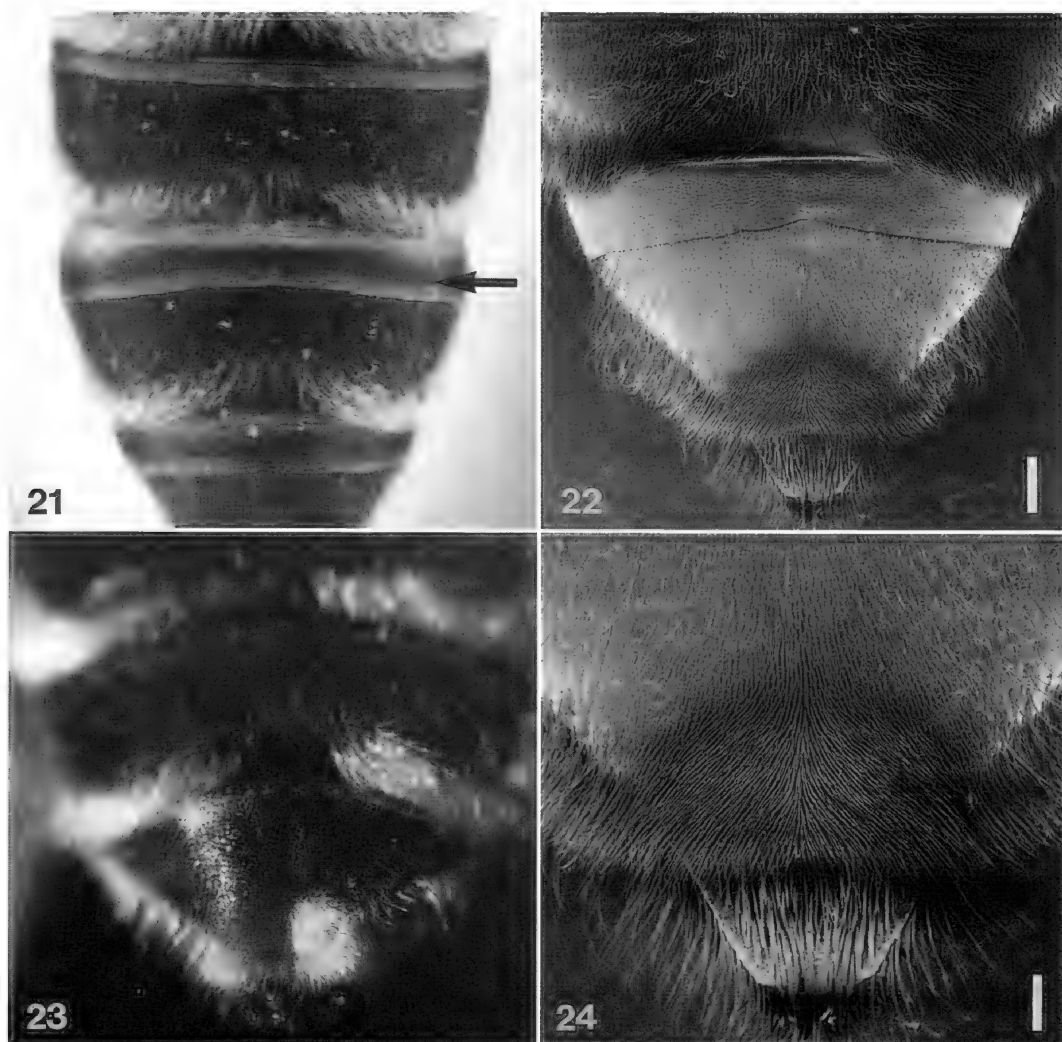


Figs. 14–20. *Brachynomada (Brachynomada) scotti*. 14. Male genitalia, dorsal (left) and ventral (right) views. 15. Same, lateral view. 16. S7 of male, ventral view. 17, 18. S8 of male, ventral and lateral views, respectively. 19. Oocyte, lateral view. 20. Apex of S6 of female, dorsal (below) and ventral (above) views. Scale (=0.1 mm) in lower right refers to fig. 20; scale (=0.1 mm) in middle right refers to all other figures.

ocular carina absent. Gena moderately narrow, its maximum width in lateral view about 0.6 times maximum eye width measured at right angles to posterior eye margin (less than 0.5 times in *B. roigi*). Antennal scape normally long, somewhat flattened. Mandible tapering to simple apex, inner dorsal edge without subapical projection (in *B. roigi*, mandible similar, except with small, obtuse, pointed, inner projection arising from upper margin about $\frac{2}{3}$ way to apex; this projection virtually absent in *B. scotti*). Maxillary palpus five-segmented, somewhat more than $\frac{1}{3}$ length of galeal blade; segment 2 longest;

segment 5 somewhat longer than segment 3 or 4; segment 1 of labial palpus almost 2 times longer than segment 2.

Mesoscutum with median and parapsidal lines only slightly impressed; mesoscutellum only faintly depressed along midline (this feature difficult to see on fresh specimens because of dense vestiture); mesepisternal scrobe in deep depression. Forewing with three submarginal cells; apex of marginal cell pointed, on wing margin. Forebasitarsus with apical $\frac{1}{4}$ narrowed along inner side, this area covered by long parallel hairs arranged as linear fringe. Hind coxa with pronounced longitudinal carina



Figs. 21–24. Metasomas of female *Brachynomada* (*Brachynomada*) *scotti*, dorsal views. **21.** Light micrograph of T3–T5 protracted, showing pale gradular lamellae and, on T4, dark line of gradular base (arrow) where lamella attaches to tergum. **22.** SEM micrograph of protracted, coated apex, showing posterior edge of gradular lamella; scale = 200 μm . **23.** Light micrograph showing differential refraction of pseudopygidial setae when specimen illuminated from side. **24.** SEM micrograph showing hair pattern of pseudopygidium; scale = 100 μm .

along mesal dorsal edge and strong carina along outer dorsal edge. Hind femur without basal, ventral, thornlike projection but with ventral surface bearing obtuse angle as seen from in front or behind about 2/3 way to apex; outer apex of hind tibia ending in curved, flared ridge, without projecting point at anterior end; apex of tibia normally wide, with two well-developed apical spurs.

Graduli of anterior terga and sterna produced as distinct, clear, thin, posteriorly di-

rected lamellae (not just carinae) that lie close to postgradular areas (as in figs. 21, 22) (see Morphology, above). Pygidial plate (T7) apically rounded. Median apical triangle of metasomal S1 little produced, with sides formed by rounded ridge; surface of triangle with some recumbent, plumose setae and longer, more erect plumose setae. S7 with apical process gradually broadening toward apex in ventral view (fig. 16), its apex much broader than that of S8; S8 with median pro-

cess elongate, gradually widening toward apex in ventral view; its apex truncate as seen in lateral view (fig. 18). *Dorsal and median processes*⁶ of gonostylus elongate, dorsal process longer than gonocoxite and penis valves as seen in lateral view (fig. 15); setae of dorsal process arising along distal half; ventral process of gonostylus⁵ projecting about as far as gonocoxal lobe in ventral view (fig. 14); setae of inner lobe tending to be shorter and finer than those of outer lobe and dorsal process; setae of ventral process moderately short and fine, arranged in linear fashion.

Color. Head, mesosoma, and metasoma very dark brown to black, except lateral pronotal lobes and distal parts of leg segments vaguely ferruginous. Wings infuscated to greater extent than those of *B. roigi*, with apical area of forewing especially dark; wing veins and stigma blackish brown.

Integumental texture and vestiture. Compound eyes without hairs. Integument of frons below ocelli smooth, with moderately dense, rather fine punctures one to two puncture-widths apart; clypeus, paraocular, and supraclypeal areas with dense, plumose, recumbent, grayish-white (with slight golden tinge) setae that nearly obscure integument on fresh specimens. Scape and pedicel more densely covered with fine setae than those of *B. roigi*. Integument of mesoscutal disc tessellate, semidull between fine punctures; these punctures evenly spaced, approximately one puncture-width apart, not more densely grouped near midline or parapsidal lines than elsewhere; on fresh specimens, integument partly obscured by semirecumbent, somewhat golden setae that do not appear plumose under normal magnification. Mesepisternum with vestiture gradually becoming sparse below so there is no abrupt line separating upper and lower parts. Wings densely hairy, more so than those of *B. roigi*;

these hairs forming microscopic fringe that extends beyond outer edge of forewing (in *B. roigi* forewing becoming hairless immediately before outer edge and therefore outer edge without fringe). Hind coxa with dorsal surface between outer and mesal carinae tessellate, without setae and punctures distally, but finely punctate and with short setae basally. Metasomal terga with integument of discs rather dull due to fine punctation and tessellation; these areas also with fine, nonplumose, recumbent, golden setae; whitish marginal hair bands broad on T1–T3, becoming interrupted medially on T4–T6; disc of pygidial plate mostly obscured by recumbent whitish setae.

Female. Structure. Head width 1.3–1.4 times length; width 1.7–2.0 mm; length 1.2–1.5 mm; wing length 4.4–5.0 mm; body length 5.3–8.0 mm.

As described for male, except for following: Inner margin of eyes converging only slightly below; eye-convergence index 0.90–0.96. Clypeal carina absent; clypeal disc and supraclypeal area nearly flat, contrasting with convexity of same areas of female *B. roigi*; interantennal distance distinctly greater than antennocular distance (these distances subequal in *B. roigi*). Paraocular carina extending only short distance from anterior mandibular articulation to eye.

Forebasitarsus with apical 1/4 not narrowed and without special setae (male features only). Outer apex of hind tibia ending in flared, obtusely rounded projection.

Apex of S6 (fig. 20) bifid, with deep median cleft; each ramus with row of stout, short setae laterally on ventral surface and with approximately six long, stout setae as well as short, more slender setae arising medially at base of cleft; long setae arising from dorsal surface and extending posteriorly somewhat beyond rami.

Color. As described for male.

Integumental texture and vestiture. As described for male, except for following: Paraocular areas with dense recumbent setae, but median part of clypeus and paraocular area less densely setose even on fresh specimens, so integument more or less visible; these median areas even more denuded on older specimens, hence flattened nature of these areas becoming shiny and even more

⁶ Michener (1996) termed the median process of the gonostylus as used here and by Ehrenfeld and Rozen (1977) as the ventral (or lower) gonostylus. He pointed out that it was also called the parapsidal lobe by Roig-Alsina and Michener (1993) and Alexander and Michener (1995). By whatever name it is called, this process is distinct from, and should not be confused with, the ventral process of the gonostylus used here and by Ehrenfeld and Rozen (1977).

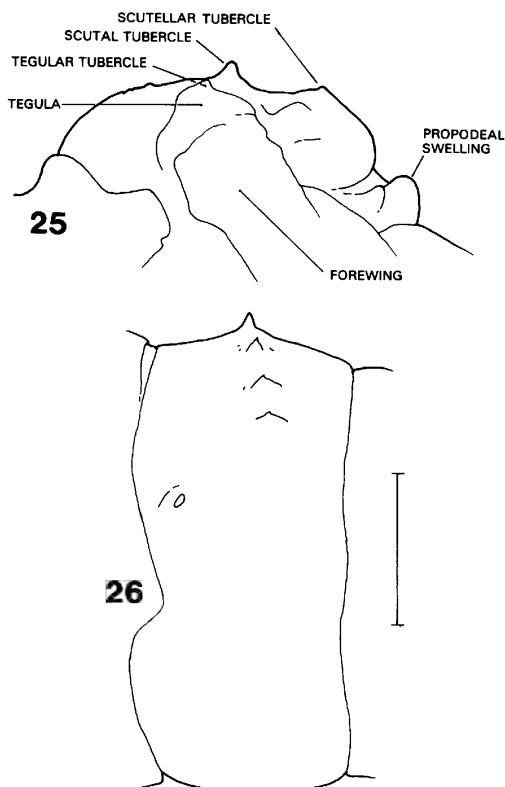
pronounced. Scape shiny, weakly punctate. Integument of mesoscutal disc smooth (non-tessellate) between moderately dense, moderately fine, evenly spaced punctures; this area with fine golden pile on fresh specimens but pile worn away on older specimens so that mesoscutum appears shiny. Middle and hind trochanters and femora with moderately dense, long, apically curved setae that bear very short branches so as to appear almost simple. Metasomal integument dullish as described for male, hence in female contrasting with shiny median facial region and mesoscutal disc; marginal pale hair bands broad, tending to be complete on T1–T4; pseudopygidial area, like that of other known *Brachynomadini* except for *Kelita*, transversely oval with short setae on either side of midline directed posterolaterally (fig. 24); hence, each half of pseudopygidial area differentially reflective (fig. 23) when illuminated from the side; apical setae of S6 described above.

HOLOTYPE: Male, allotype, 4 male and 1 female paratypes: **PERU, Lima Dept.:** 8 km E. Chosica, VII-8-1995 (J. G. Rozen and A. Ugarte), *Exomalopsis* nest site; 3 male and 2 female paratypes, same except VI-23-1995; 8 male paratypes, same except VII-2, 3-1995; 3 male and 13 female paratypes, same except VII-3-1995 (4 preserved in Kahle's solution); 7 male paratypes, Ricardo Palma, VI-21-1995 (J. G. Rozen, A. Ugarte, and M. Laime) (no host data; this locality identical to 8 km E. Chosica); 1 pupal male paratype, cited below. **Ancash Dept.:** 1 male paratype, 57 km N.E. Chasquitambo, VI-29-1995 (J. G. Rozen and A. Ugarte). **ECUADOR, Manabí:** 1 male paratype, Garrapa, W. of Santo Domingo de los Colorados, XII-27-1970 (L. E. Peña). This species is known only from these localities (fig. 13).

The holotype, allotype, and paratypes are in the collections of the American Museum of Natural History. Paratypes are also in the Museo de Historia Natural, Lima, Peru; the Snow Entomological Division, Natural History Museum, University of Kansas, Lawrence; and the Museo de Ciencias Naturales, Buenos Aires, Argentina.

ETYMOLOGY: This species is named in honor of Scott J. Rozen-Levy.

REMARKS: Whereas the male genitalia of *Brachynomada scotti* differ from those of *B.*



Figs. 25, 26. Pupa of *Brachynomada* (*Brachynomada*) *scotti*, lateral views. **25.** Dorsum of mesosoma, showing size and distribution of tubercles. **26.** Third metasomal segment, showing dorsal tubercles. Scale (= 0.5 mm) refers to both figures.

roigi as indicated in the description, the genitalia of *B. scotti* and those of *Trichynomada roigella* illustrated by Michener (1996: figs. 11, 12) are rather similar, as are the truncated apices of S8 of these two taxa. Their terminalia differ, however, in that the male pygidial plate of *T. roigella* is notched medially rather than rounded and its penis valves are more slender.

PUPA

Figures 25, 26

DIAGNOSIS: The pupa of this species is similar to that of *Brachynomada* (*Brachynomada*) *roigi* (Rozen, 1994), differing by the features identified in the description below. Like *B. roigi*, it possesses paired scutal tubercles and can, therefore, be distinguished

from *B. (Melanomada) sidae* and *Paranomada velutina*, the only other taxa in the tribe whose pupae have been described (Rozen, 1977). All of these brachynomadine taxa lack the small, sharp-pointed, apically pigmented tubercles on the head and dorsal mesosoma characteristic of pupae of other Nomadinae that have been studied (see references in McGinley, 1989; Rozen, 1989a).

HEAD AND MESOSOMA: As described for *Brachynomada roigi*, except for following: Paired scutellar tubercles (fig. 25) less pronounced though evident. Tegular tubercle (fig. 25) present but small. Each trochanter with small apical tubercle on ventral surface; forebasitarsus with more distinct, rounded, apical swelling on posterior surface accommodating apical fringe of specialized hairs of adult male; apical swellings on fore and hind femora scarcely noticeable.

METASOMA: As described for *Brachynomada roigi*, except for following: T1–T6 with tubercles more distinct; sterna S4–S6 with paired apical swellings that are more pronounced than those of *B. roigi*, which had been overlooked.

MATERIAL STUDIED: PERU, Lima Dept.: 1 male pupa, 8 km E. Chosica, VII-3-1995 (J. G. Rozen and A. Ugarte).

LARVA

Although the larva of this species was not discovered in the *Exomalopsis* nest, the cast larval skin associated with the pupa provides some details concerning larval anatomy. Unfortunately, significant information regarding such matters as head and body shape and proportions cannot be determined. At molting, the head capsule split along the midline from the vertex nearly to the labral base. In the following description, the sequence of presentation is the same as used for the description of the larva of *Brachynomada roigi* (Rozen, 1994: 10–12).

HEAD: Integument not darkly pigmented except for epistomal, pleurostomal, and hypostomal ridges and mandibular apices and articulations; maxillary palpi and labral tubercles faintly pigmented; hypopharynx, side and top of maxilla, and apparently sides of labrum spiculate.

Possible swelling and wrinkling of vertex

unknown. Anterior tentorial pit indistinguishable on cast skin but presumably immediately adjacent to anterior mandibular articulation as judged by extremely short epistomal ridge (as also in evidence in *B. roigi*); posterior tentorial pit small, immediately below hypostomal/postoccipital ridge; this ridge gradually curving dorsally posterior to pit and becoming thinner until it nearly disappears about halfway to vertex; hence, postoccipital ridge somewhat more pronounced than that of *B. roigi*; hypostomal and pleurostomal ridges moderately well developed; epistomal ridge only evident in immediate vicinity of anterior mandibular articulation, completely absent across face between these articulations. Antennal prominence apparently weak; antennal disc and papilla moderate in size, one bearing three sensilla. Paired labral tubercles moderately long, somewhat longer than basal diameter.

Mandible slender, elongate, tapering to bladelike, sharp, simple apex; dorsal and adoral surfaces with scattered sharp denticles; outer surface with a few short setae but without setiferous tubercles; mandible as seen in adoral or aboral view S-shaped as illustrated for *B. roigi* (Rozen, 1994: fig. 9), i.e., apex curving downward (ibid.: figs. 6, 7); cusp and apical concavity scarcely differentiated; dorsal and ventral apical edges serrate; ventral apical edge with fewer teeth than dorsal edge but more teeth than illustrated for *B. roigi* (ibid.: fig. 9). Labiomaxillary region recessed and fused. Maxillary apex a simple lobe bearing conspicuous palpus that is only a little smaller than labral tubercle; labial palpus a single sensilla not on obvious projection. Salivary opening a simple hole without rim or lips.

BODY: Integument without setae, distinctly spiculate ventrally immediately behind head and in many other areas but pattern of spiculation unknown; integument without spines or sclerotized areas. Spiracles moderately large, all subequal in size; peritreme present, narrow, possibly inflexed around opening; opening apparently normally circular but on some slightly irregularly scalloped; atrium pigmented; atrial wall with linear series of fine denticles, without reticulate ridges as found in *B. roigi*; primary spiracular opening with collar.



Fig. 27. Nesting site of *Exomalopsis bruesi*. Nest entrances associated with shallow ditch between A. Ugarte and adobe wall.

MATERIAL STUDIED: One cast integument associated with pupa described above.

**BIOLOGICAL NOTES ON
BRACHYNOMADA SCOTTI
AND ITS HOST, *EXOMALOPSIS BRUESI***

The recent reclassification of the *Exomalopsini* by Silveira (1995) is adopted here.

OBSERVATIONS

Three nest entrances of the host bee, *Exomalopsis* (*Exomalopsis*) *bruesi* Cockerell (identified by F. Silveira), were discovered in Ricardo Palma (8 km east of Chosica), Lima Department, Peru, on June 21, 1995. The entrances, within 28 cm of one another, were in an unvegetated location next to a low adobe wall, fully exposed to the sun except very early in the morning (fig. 27). Two nests were excavated, the first on June 23 and the other on July 2 and 3. Each was occupied by numerous host bees, which were easily collected in the early cool mornings as they slowly crawled from entrances, occasionally

with individuals of their cleptoparasite (*Brachynomada scotti*), of a rhipiphorid parasitoid (*Macrosiagon vittatum* [Erichson], tentatively identified by Zachary Falin), and of a dipteran (tentatively identified as the conopid *Zodion*). Two of the nest entrances were in the vertical face of a shallow irrigation channel (fig. 17), and the other was on a horizontal surface. Neither nest was excavated fully, but there was no indication that they anastomosed, despite their proximity.

Both main tunnels were 4.0–4.5 mm in diameter, open, and meandering downward. In one nest numerous cells, arranged singly (i.e., not in linear series), were encountered between 35 and 45 cm below the surface and extended laterally from the entrance about 20 cm. They were roughly 7–8 mm long and 5 mm in maximum diameter. Oriented with long axis 20–80° from horizontal, rear end down, they possessed a smooth lining. Cell closures were a spiral of four to five coils, concave on the inside, with a smooth concave surface on the outside. The second nest was followed to a depth of 100 cm, at which

point investigation was discontinued. Although it branched a number of times, relatively few cells were encountered, and most of these were vacated. Hence, the two nests differed in cell depth.

Numerous pupae and only a few fresh, loaflike, yellowish food masses were encountered in June. Three loaves measured 4.4–4.7 mm long, 3.1–3.2 mm at maximum height (toward rear), and 3.0–3.2 at maximum width (at middle). Like those of other species, the loaf was somewhat flattened on the sides, the rear was convex, and the top surface was gently convex from the high point in the rear to the lower front end. This species did not construct a foot at the front as do some *Anthophorula* and *Exomalopsis* (Rozen, 1984; Rozen and Snelling, 1986). The entire bottom surface adhered to the cell floor, and the egg was laid on the front half of the loaf in the midsagittal plane of the cell, as is characteristic of many *Exomalopsis*, *Anthophorula*, and *Eremapis* (Neff, 1984).

As they crawled, feeding larvae of *Exomalopsis bruesi* channeled the surfaces of the food masses, and they started defecating before they had fully consumed the loaf. Feces, deposited as moist pellets, were always placed on the cell wall in the rear half of the cell. The thickest part of the deposit was rearmost in the cell, not unlike that diagrammed for noncocoon-spinning *Anthophorula sidae* (Rozen, 1984: fig. 31). *Exomalopsis bruesi* does not spin cocoons, for no pupa was encased in a cocoon and mature larvae did not have projecting labia with projecting salivary lips.

No special interactions were noted between adult *Exomalopsis* and adults of *Brachynomada* as they emerged from the nest entrances in the cool morning; all emerging individuals were sluggish and seemed to ignore one another.

A single cell of *Exomalopsis bruesi* contained an immature *Brachynomada scotti*. The pupa and cast larval skin, described above, were retrieved, and two egg insertion holes were found in the cell wall near the closure end. Each of these consisted of an oblique slit in the cell lining, with a flap of lining and soil, about 0.5 mm wide at the base, hinged to it. Almost certainly an egg of *B. scotti* had been inserted under each flap,

as discussed by Rozen (1994: 7) for other brachynomadines and some other Nomadinae. No cast skins of first instars were recovered. Fecal material, in more or less discrete pellets, was restricted to the rear one-quarter to one-third of the cell. This species, like all other known Nomadinae (sensu Roig-Alsina and Michener, 1993), is incapable of cocoon spinning.

One of the females of *Brachynomada scotti* preserved in Kahle's solution was dissected to inspect its ovaries and oocytes. Lack of wing wear suggests that she had recently emerged. The following statistics are comparable to those of other known Brachynomadini (Rozen, 1994: table 1): egg index 0.28; total number of mature oocytes 14; mature oocytes per ovariole 0.78; number of ovarioles 9:9; oocyte length and maximum diameter 0.54 mm and 0.21 mm (width 2.57 times length). Mature oocytes (category A of Iwata, 1955) were identified through follicular tissue by their slightly yellowish cast compared with whitish immature oocytes and by their shiny chorions. Dissected oocytes (fig. 19) possessed a smooth, transparent chorion and a hooked projection at the anterior end. Like the oocytes of other known Brachynomadini (Rozen, 1994), they were short relative to their girth and somewhat more pointed at the anterior end than at the rear, with the broadest diameter posterior to the middle, as seen in lateral view. The very high value for mature oocytes per ovariole may be the result of the female being fresh and/or of the fact that *Exomalopsis* cell construction and provisioning appeared at a seasonal nadir. The cleptoparasite female simply may not have had an opportunity to oviposit.⁷

The fact that so many cells were vacated or contained pupae rather than an assortment of life stages suggests that the adult population size and nesting activity vary seasonally, probably in response to the flowering season. The rarity of *Brachynomada* immatures in nests (adult cleptoparasites were quite abun-

⁷ Upon reading this manuscript, C. D. Michener was skeptical of this explanation because resorption of oocytes is so common in Hymenoptera. However, I have been unaware of evidence of resorption in the ovaries of cleptoparasitic bees.

dant) also supports this idea. *Exomalopsis bruesi* is distributed widely, at least on the western slope of the Andes in the vicinity of Lima and northward, where it was encountered at numerous localities collecting pollen from a variety of plants.

The nesting area was again visited in May 1996, but by this time an adobe house had been constructed over it.

DISCUSSION

Beyond the new cleptoparasite association, the biological information concerning *Exomalopsis bruesi* is not unique compared with what is known about other species of *Exomalopsis* and *Anthophorula* (see Rozen, 1984; Rozen and Snelling, 1986). However, uncommon features of these two genera include the facts that the food loaf of *E. bruesi* lacks a foot (also true for *E. similis* and *E. globosa*, Raw, 1977) and that the larvae of *E. bruesi* are incapable of cocoon spinning.

Among species about which I have information, all *Anthophorula* (including *A. completa* [Cockerell], NEW RECORD) shape the larval food loaf with a foot (Rozen, 1984; Rozen and Snelling, 1986). Such a foot has been recorded for only one species of *Exomalopsis*, *E. solidaginis* Cockerell (Rozen, 1984; Norden et al., 1994). However, the form of the food mass of *E. aureopilosa* Spinola is apparently quite different from all other species (Zucchi, 1973). The food mass of the third exomalopsine genus, the monotypic *Eremapis*, does not have a distinct foot (Neff, 1984; Rozen, unpublished field notes), but samples of uneaten food loaves in the collections of the American Museum of Natural History show that the front edge is sharply angled in lateral view, a suggestion (corroborated by field notes) of a foot. This probably implies that females of this species manipulate provisions very much as do those species that shape provisions to have a foot. However, there is no information as to how females of any exomalopsine shape the food masses.

So far as is known, *Anthophorula* have larvae capable of cocoon spinning, although several multivoltine species apparently have generations that skip cocoon spinning (Rozen, 1984). Some species of *Exomalopsis* spin

cocoons, but others are incapable (recessed labiomaxillary regions, reduced salivary lips) of doing so (Rozen, 1984; Norden et al., 1994). *Eremapis* routinely spins a distinctive cocoon (Neff, 1989; Rozen, unpublished field notes).

The certain association of *Brachynomada scotti* as a cleptoparasite of *Exomalopsis* (*Exomalopsis*) *bruesi* is of interest because other pairings of *Brachynomada* sensu stricto with hosts have involved only the panurgine genus *Psaenythia* (Rozen, 1994). On the other hand, all associations of the subgenus *Melanomada* as well as of the North American *Triopasites* and *Paranomada* have been with species of *Exomalopsis* and *Anthophorula*, as can be seen in table 1. Hence, *B. scotti* bridges a gap in the sense that all known genera and subgenera of the Brachynomadini, with the exception of *Kelita*, have species that attack *Exomalopsis* and *Anthophorula*. Considering the taxonomic separation of *Psaenythia* from the exomalopsine genera, one can speculate that the communal nests of the exomalopsines and those of *Psaenythia* (with the possible exception of *P. annulata* [Gerstaecker]; see Rozen, 1989b) may somehow be the basis for these host preferences.

Among the various associations of the brachynomadines with *Exomalopsis* and *Anthophorula*, this is the first to involve a member of the subgenus *Exomalopsis*.

Table 1 is a listing of the species of the Exomalopsini (by genus and subgenus) that are known to be attacked by nomadine cleptoparasites. It shows that two subgenera (*Anthophorula*, *Anthophorisca*) of *Anthophorula* host brachynomadines. A single unparasitized nest of the monotypic *Anthophorula* subgenus *Isomalopsis* was examined at 11 km north of Cadillal, Tucumán Province, Argentina, in 1989 (NEW INFORMATION), unconvincing evidence that the subgenus is cleptoparasite-free. Two *Exomalopsis* subgenera (*Stilbomalopsis*, *Exomalopsis*) are parasitized by brachynomadines, but nests of the other two subgenera (*Phanomalopsis*, *Diomalopsis*) have yet to be discovered.

Table 1 also shows that, with the exception of *Anthophorisca*, subgenera subject to brachynomadine cleptoparasitism are also attacked by *Nomada*.

Eremapis is apparently not attacked by ei-

TABLE 1
Cleptoparasitic Associations between Subgenera and Species of the Exomalopsini and Species of the Nomadinae

(Modified and updated from Rozen, 1984: table 2. All associations based on cleptoparasitic immatures being collected from nests, unless indicated otherwise. Classification of the Exomalopsini follows that of Silveira, 1995.)

Exomalopsini	Nomadine Taxon	Source
<i>Anthophorula</i> s.l.		
<i>Anthophorula</i> s.s.		
<i>compactula</i> (Cockerell)	<i>Triopasites penniger</i> (Cockerell)	Rozen, 1977
<i>completa</i> (Cockerell)	<i>Triopasites penniger</i> (Cockerell)	New record
<i>crenulata</i> (Timberlake)	<i>Nomada gutierreziae</i> Cockerell ^a	Parker, 1984
<i>Anthophorisca</i>		
<i>consobrina</i> (Timberlake)	<i>B. (Melanomada) sidaefloris</i> (Cockerell)	Rozen, 1977
<i>nitens</i> (Cockerell)	<i>B. (Melanomada) annectens</i> Snelling and Rozen ^b	Rozen and Snelling, 1986
<i>sidae</i> (Cockerell)	<i>B. (Melanomada) sidaefloris</i> (Cockerell)	Rozen, 1977
<i>Exomalopsis</i> s.l.		
<i>Stilbomalopsis</i>		
<i>solani</i> Cockerell	<i>Nomada gutierreziae</i> Cockerell	Norden et al., 1994
	<i>Paranomada velutina</i> Linsley	Rozen, 1977
<i>solidaginis</i> Cockerell	<i>Paranomada nitida</i> Linsley and Michener	Rozen, 1984
	<i>Paranomada californica</i> Linsley ^c	Linsley, 1945
<i>Exomalopsis</i> s.s.		
<i>aureopilosa</i> Spinola	<i>Nomada</i> prob. <i>tomentifera</i> Ducke ^d	Zucchi, 1973
<i>bruesi</i> Cockerell	<i>Brachynomada scotti</i> Rozen	Present study
<i>globosa</i> (Fabricius)	<i>Nomada cubensis</i> (Cresson) ^e	Raw, 1977
	<i>Nomada pilipes</i> (Cresson) ^e	Raw, 1977
<i>similis</i> Cresson	<i>Nomada cubensis</i> (Cresson) ^e	Raw, 1977
	<i>Nomada pilipes</i> (Cresson) ^e	Raw, 1977

^a Immatures not collected, but association certain, based on dead, unemerged cleptoparasites in cells and fecal pattern of larvae.

^b Identified as *Hespernomada melanantha* Linsley in Rozen (1984) and as *Melanomada* sp. in Rozen and Snelling (1986).

^c Association probable. P. H. Timberlake suggested that *Exomalopsis solidaginis* (as *verbesinae* Cockerell) might be the host of *Paranomada californica* because they flew together and shared a striking similarity (Linsley, 1945).

^d The identification of this species is uncertain. Upon reading this manuscript, A. Roig-Alsina (personal commun.) stated, "According to its original description, and also as it has been recognized by subsequent authors (e.g., Friese, 1908), *N. tomentifera* Ducke is a species of *Brachynomada*." However, Zucchi had kindly sent me two larvae labeled: *Nomada* probably *tomentifera* from nest of *Exomalopsis aureopilosa*. BRAZIL, sp., Ribeirão Preto, May 10, 1968 (R. Zucchi). These larvae, now in the collection of the American Museum of Natural History, are clearly *Nomada* and not brachynomadine.

^e Association highly probable. Numerous cleptoparasites seen entering nest, but immatures not recovered.

ther *Nomada* or brachynomadines. Neff (1984) studied several large nesting sites of this genus and saw no cleptoparasite activity (personal commun.). I, too, studied sites of this species, at Pampa Vieja, near San José de Jáchal, San Juan Province, and at Guan-

dacol, southwest of Unión, La Rioja Province, Argentina, in 1993, without sighting cleptoparasitism (NEW INFORMATION). Although not proof, so many observations strongly suggest that *Eremapis* may be cleptoparasite-free.

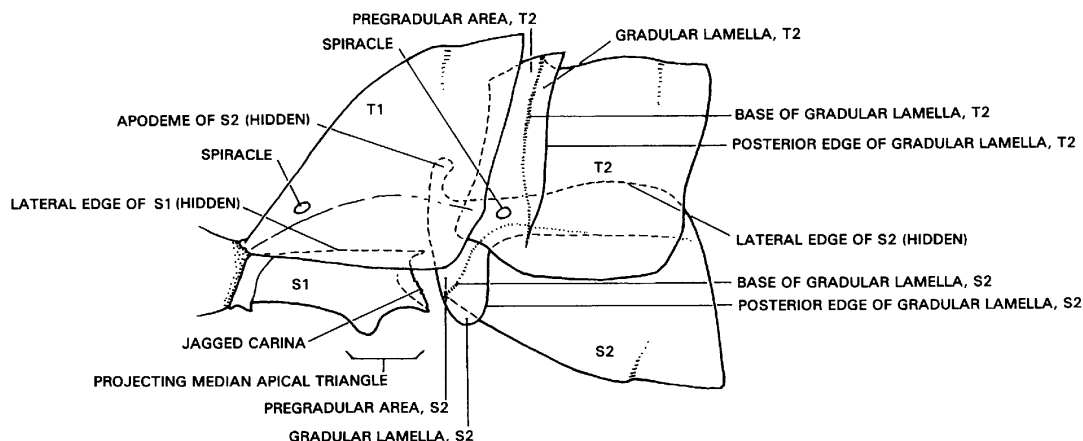


Fig. 28. Diagram of male of *Triopasites penniger*, first two metasomal segments, slightly protracted, lateral view, setae omitted to show projecting median apical triangle of S1 and gradular lamella of T2 and S2.

Of all the known host associations of the Brachynomadini, only *Kelita* has not been found to attack nests of exomalopsines; its hosts are solitary or communal, as discussed by Rozen (1994). It will be interesting to learn the host associations of *Trichonomada* and *Spinokelita* and what cleptoparasites are associated with other groups of exomalopsines.

TRIOPASITES LINSLEY

The morphological parameters of the genus are greatly modified compared with such accounts as those of Michener (1996) because of the synonymy (listed below) of all species of *Triopasites* described to date and because of the recognition of *T. spinifera*. Most features thought to be generic heretofore have become specific.

DESCRIPTION: Anterior mandibular articulation only slightly farther from eye than posterior articulation. Maxillary palpus short, no more than one-third length of galeal blade, with five or fewer segments. Eyes appearing glabrous but, under high magnification, with scattered fine setae that are much shorter than those of *Trichonomada*. Mesosoma and base of metasoma broad in dorsal view, slightly dorsoventrally flattened but far less so than in *Paranomada*. Forewing with apex of marginal cell narrowly to very narrowly rounded, on wing margin or slightly removed from it; forewing normally with three submarginal

cells, but some specimens of *Triopasites penniger* with only two. Hind femur normal, without basal thornlike projection ventrally.

Graduli of most terga and sterna projecting posteriorly as thin, transparent lamellae (as in figs. 21, 22), in contrast to nonlamellate gradular ridge of *Kelita* sensu lato. Median apical triangle of S1 projecting downward; lateral edges of triangle directed posteriorly as lamellate carina (in male of *T. penniger*, sides of triangle fused into single, very strongly projecting, jagged carina). Pseudopygidial area of female with posterolaterally directed, simple setae on each side (as in fig. 24). Female S5 produced posteriorly as a setose median projection in ventral view, not broadly rounded as in *Trichonomada*. Male S8 (figs. 32, 33, 39, 40) posteriorly with attenuated median process that is narrowly rounded apically, not with short, tapering, median process that is broadly rounded apically as in *Melanomada*. Dorsal and median processes of gonostylus short; dorsal process not extending as far as penis valve and shorter than gonocoxite in lateral view (figs. 30, 37); this process bladelike in lateral view, very broad immediately beyond attachment to gonostylus and then steadily narrowing to apex; because of small size, median process not clearly (but possibly) separated into inner and outer lobes; ventral process large, bent mesad, its posterior surface with numerous long setae; gonocoxal lobe scarcely visible in

ventral view (figs. 29, 36) because of large size of ventral process; setae of ventral process tending to be as long as those of dorsal and median processes; volsella weakly pigmented. Penis valve robust, with apical part angled abruptly from basal part as seen in dorsal and ventral views (figs. 29, 36).

Triopasites penniger (Cockerell)

Figures 28–36

Nomada penniger Cockerell, 1894: 235–236.

Triopasites penniger (Cockerell), Rodeck, 1951: 1205.

Nomada pasitura Cockerell, 1935: 6. NEW SYNONYMY.

Triopasites pasitura (Cockerell), Rodeck, 1951: 1207.

Triopasites timberlakei Linsley, 1939: 9–10. NEW SYNONYMY.

Triopasites micheneri Linsley, 1943: 101–102. NEW SYNONYMY.

Triopasites laguna Linsley, 1943: 102–103. NEW SYNONYMY.

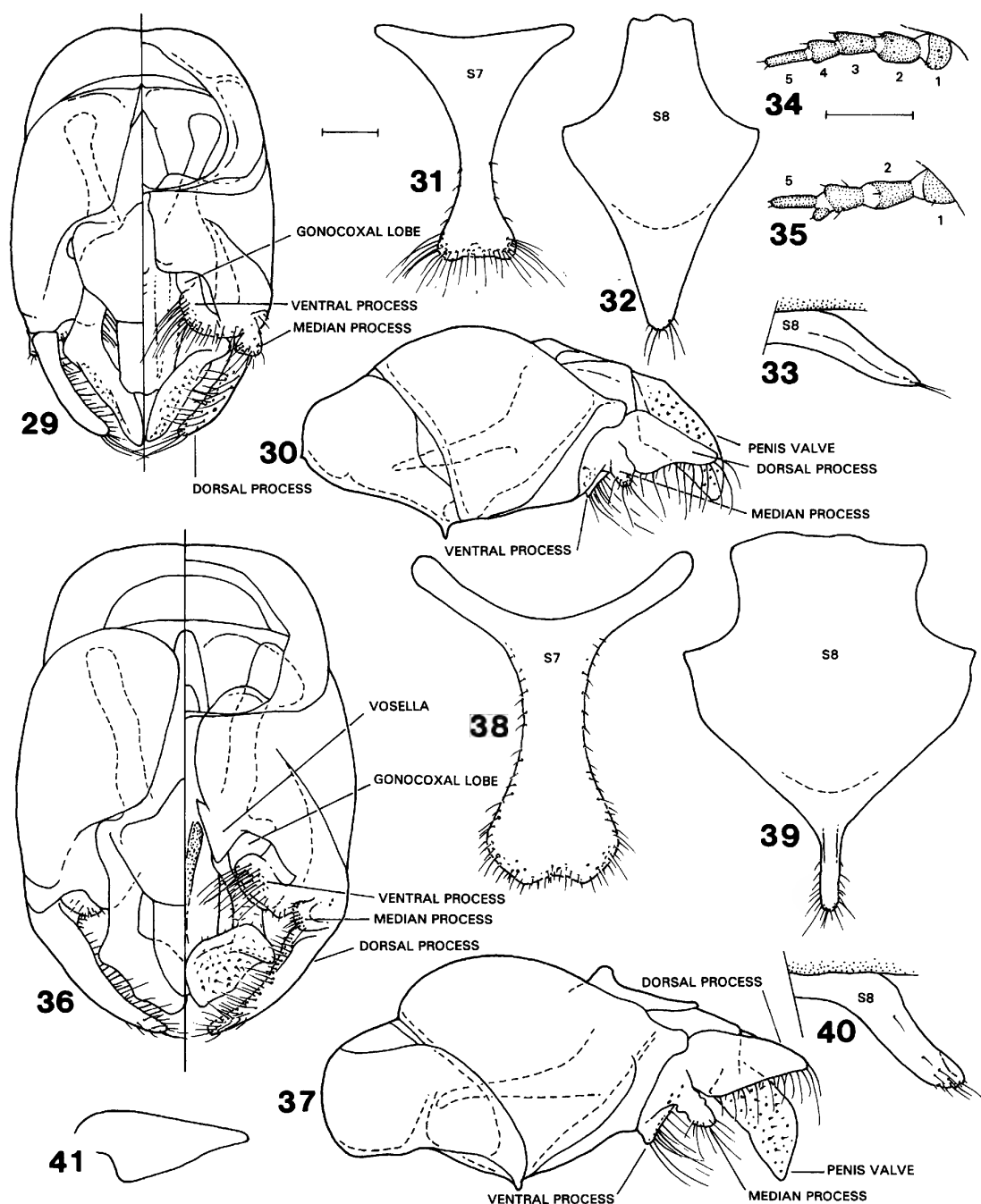
Triopasites was proposed by Linsley (1939) to accommodate a new species, *T. timberlakei* Linsley, based on a female specimen from Riverside, California. Several years later, Linsley (1943) described two more species in the genus, *T. micheneri* (holotype female) from Tucson, Arizona, and *T. laguna* (holotype male) from La Laguna, Sierra Laguna, Lower California (presumably La Laguna, Baja California Sur, a fishing village on Laguna de San Ignacio). Subsequently, Rodeck (1951) assigned two previously described species to *Triopasites*: *Nomada penniger* Cockerell (1894), known from a single male specimen from Las Cruces, New Mexico, and *N. pasitura* Cockerell (1935), based on a male (incorrectly recorded as a female) from Bexar County, Texas. Differences among these nominal species involved integumental color and number of segments in the maxillary palpus, although broad geographic range and limited collections must have played a role in confusing species distinctiveness. Linsley (1943) suggested that *T. laguna* might be the male of *T. micheneri* or *T. timberlakei*.

Acquisition of larger series and of specimens from localities intermediate between the type localities over the last 40 years has led to review of these nominal species. After

studying these specimens and examining all types, I recognize only a single, wide-ranging, polychromatic species. The species is now known from the west coast of southern California (San Diego and Riverside Counties) and southern Nevada to the tip of Baja California Sur, across southern Arizona and New Mexico to Bexar County, Texas, and from Sinaloa across Chihuahua and Coahuila to Llera and “Jiminez” (presumably Jiménez Santander), Tamaulipas (fig. 42). Adults have been collected every month from April 2 to October 30. It is unknown, however, whether the species is multivoltine or whether it is univoltine with different subpopulations (perhaps associated with different hosts) active at different seasons.

Reported differences among the nominal species involved number of segments in the maxillary palpi. However, the maxillary palpi are very small and difficult to observe on dried specimens. Dissected specimens reveal that these palpi are probably basically five-segmented, with the first segment (figs. 34, 35) extremely short and sclerotized on only one side so that the sclerite does not ring the segment. On dried specimens, this sclerite often cannot be detected, although it is also possible that it is actually lost in some cases. Other segments vary in length, so that on dried specimens they appear to be lost and indeed may actually be lost. Figure 35 shows a specimen with segment 4 reduced to a lobe attached to one side of the palpus; other specimens from the same locality clearly have five segments similar to those shown in figure 34. No geographic pattern or correlation with other characters can be detected. Hence, the length of this minute palpus and the number of segments involved appear to be quite variable, perhaps in the absence of selection pressure.

Coloration of specimens varies considerably, with some being almost totally mahogany brown (close to black) while others are pale reddish. Contrast between the extremes is striking, but all intermediate degrees of pigmentation can be found. Most specimens exhibit a dark reddish-brown vertex and partly reddish-brown mesosoma and metasomal apex. Other areas are paler reddish. The darkest specimens are from Baja California,



Figs. 29–41. 29–35. *Triopasites penniger*. 29. Male genitalia dorsal (left) and ventral (right) views. 30. Same, lateral view. 31. S7 of male, ventral view. 32. S8 of male, ventral view. 33. Apex of same, lateral view. 34, 35. Maxillary palpi of two specimens, showing variation. 36–41. *Triopasites spinifera*. 36. Male genitalia, dorsal (left) and ventral (right) views. 37. Same, lateral view. 38. S7 of male, ventral view. 39. S8 of male, ventral view. 40. Apex of same, lateral view. 41. Dorsal process of gonostylus in full lateral profile. Left scale (=0.1) refer to figures 29–32 and 36–41; right scale (=0.1) refers to figures 34, 35.

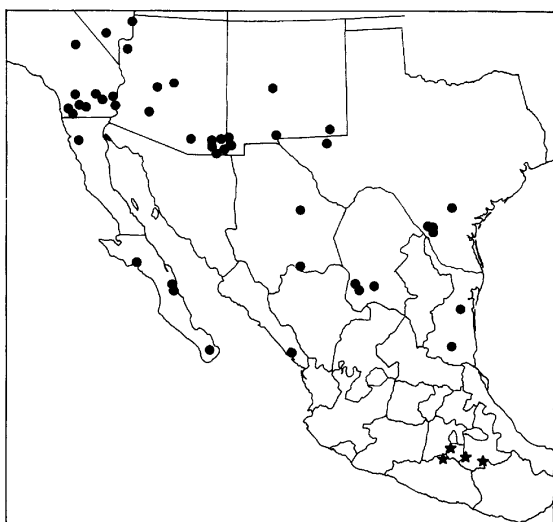


Fig. 42. Southwestern United States and northern Mexico, showing distributions of *Triopasites penniger* (circles) and *T. spinifera* (stars).

and the lightest ones come from southern Arizona and New Mexico.

The density of pubescence varies to some degree, but pubescence patterns and features of male genitalia and apical sterna (figs. 29–33) are uniform.

Triopasites spinifera, new species

Figures 36–42

Characters in boldface agree with those of *Triopasites penniger* and support the assignment of this species to *Triopasites*. Italicized characters are diagnostic for distinguishing *T. spinifera* from *T. penniger*.

DIAGNOSIS: Males can be immediately separated from those of *T. penniger* on the basis of their highly modified hind-tibial apex (fig. 2), a unique condition for any New World cleptoparasitic bee north of the equator. This peculiar modification, almost certainly derived *de novo*, is also found on the male of the Argentine *Kelita* (*Spinokelita*) *argentina*, described above. Because of their blackish coloration and different pubescence pattern of the mesepisterna and metasomal sterna, males and females of *T. spinifera* will not be easily confused with those of *T. penniger*.

DESCRIPTION: Male. Structure. Head width (maximum distance between outer eye margins) 1.4 times length (vertex to lower mar-

gin of clypeus); width 2.1–2.3 mm; length 1.6 mm; wing length 4.7–4.9 mm; *body length* 7.2–8.5 mm (in *T. penniger*, body length 5.5–7.0 mm).

Median ocellus either touching upper orbital tangent or less than 1/2 ocellar diameter removed from it. Inner orbits converging below; eye-convergence index 0.82–0.87. Clypeus with long, low carina laterally; clypeal disc and supraclypeal area slightly convex; interantennal area somewhat produced along midline and with weak midline ridge that extends partway to median ocellus; labral disc broadly concave; apical labral margin with irregularly denticulate ridge. Anterior mandibular articulation almost as close to eye as posterior articulation. Paraocular carina absent. Gena moderately wide, its width in lateral view more than 0.7 times maximum width of eye measured at right angles to posterior eye margin (less than 0.6 times in *T. penniger*). Antennal scape normally long, somewhat flattened. Mandible tapering to simple apex, inner dorsal edge without subapical projection (in *T. penniger*, mandible similar except with small, obtusely pointed inner projection on upper margin about 2/3 way to apex). Maxillary palpus five-segmented (in *T. penniger*, palpus with five or maybe fewer segments; palpifer-like segment 1 very small but present at least in some cases though easily overlooked because sclerotized only on outer surface and small; other segments possibly coalesced but usually present and distinct though small and sometimes telescoped); **palpus very short, 1/3 or less (less than 1/4 in *T. penniger*) length of galeal blade**; segment 2 longest; segments 3–5 roughly subequal in length; segment 1 of labial palpus more than 2 times longer than segment 2.

Mesoscutum obscured but apparently without deeply impressed median and parapsidal lines, and anterior part of median line raised on some specimens; mesoscutellum faintly depressed along median line; mesepisternal scrobe in moderate depression. Forewing with three submarginal cells; apex of marginal cell very narrowly rounded to almost pointed, nearly on wing margin to being bent away by vein width. Forebasitarsus unmodified apically, setae along apical inner side, though slightly thicker, not appreciably

longer than more basal setae. Hind coxa with conspicuous longitudinal carina on mesal dorsal edge as well as strong carina along outer dorsal edge. Hind femur normal, without basal, ventral, thornlike projection; *inner apex of hind tibia* (fig. 2) *extremely broad, produced into long curved spine*; outer apex ending in slightly flared ridge without projecting point at anterior end; *hind tibial spur reduced to one long spur on holotype and four male paratypes*; on specimen from 15 km W.S.W. of Izucar, right hind tibia with single spur short, less than length of midtibial spur and not extending as far as apex of inner curved spine; left tibia of same specimen with two spurs, posterior one long, anterior one even shorter than right hind tibial spur.

Graduli of anterior terga and sterna produced as distinct, clear, thin, posteriorly directed lamellae (not just carinae) that lie close to postgradular areas (see Morphology, above). Pygidial plate (T7) apically rounded. **Median apical triangle of S1 projecting downward; lateral edges of triangle directed posteriorly into lamellate carina similar to, though distinctly less pronounced than, that of *Triopasites penniger*** (in other Brachynomadini median triangle of S1 projecting little downward; lateral edges rounded in *Kelita* sensu lato, *Paranomada*, *Trichonomada*, and some *Brachynomada* sensu lato; in other *Brachynomada*, edges carinate or weakly so, but not lamellate); surface of triangle with dense, semi-erect, plumose setae. S2 with margin not depressed (in *T. penniger*, margin depressed). S7 (fig. 27) with apical process more nearly parallel-sided at base, widening toward apex, its apex broad, bilobed (in *T. penniger* [fig. 31], apical process gradually narrowing toward apex before gradually broadening; apex narrower, scarcely notched medially); S8 (fig. 39) with basal apodeme very broad, much more so than that of *T. penniger* (fig. 32); sternum and apical process at base gradually narrowing as seen in ventral view; apical process elongate, with distal part narrow, parallel-sided in ventral view, apically rounded with dorsal longitudinal keel in lateral view (fig. 40) (in *T. penniger*, apical process gradually narrowing apically for its entire length [fig. 32], more pointed in lateral view [fig. 33]).

Genital capsule and its appendages as described for genus, except for following: volsella (fig. 36) apically pointed (in *T. penniger*, volsella more closely united with gonocoxite, so boundaries difficult to determine); ventral median ridge of penis (fig. 36) spiculate at base (in *T. penniger*, nonspiculate).

Color. Head, mesosoma, and metasoma very dark brown to black, except tarsi and mandibular apices tending to be somewhat ferruginous; in addition, lateral pronotal lobes of one specimen ferruginous and lobes of two others with ferruginous spots; one specimen with femorotibial joints vaguely ferruginous; tegulae dark brown (in *T. penniger*, labrum, much of lower face, much of mesothorax and legs, as well as base of metasoma ferruginous; ferruginous areas grading to brown or dark brown; tegulae medium brown to ferruginous). Wing moderately infuscated (more so than in *T. penniger*), with apical part more darkly pigmented, and with darker area at apex of marginal cell; veins and stigma dark brown.

Integument texture and vestiture. Compound eyes with widely scattered microscopic setae, which are so minute they would have gone unnoticed if setose eyes had not been reported for *Trichonomada*. Integument of frons below ocelli densely, deeply punctured; punctures irregularly spaced but about $\frac{1}{4}$ – $\frac{1}{2}$ puncture-widths apart; area between punctures smooth, shiny (in *T. penniger*, punctures somewhat finer, about one puncture-width apart); clypeus, paraocular and supraclypeal areas with dense, white, recumbent pubescence mixed with suberect, fine setae, this pubescence nearly obscuring integument on fresher specimens. In general, punctuation of mesosoma coarser, more dense than that of *T. penniger*; mesoscutal disc with punctures tending to be less than one puncture-width apart; interspaces shiny; on fresh specimens disc with brown, suberect pubescence that obscures integumental punctuation. *Mesepisternum thickly beset with suberect, white pubescence that partly obscures integument above and becomes denser below so that lower part in lateral view completely obscured* (in *T. penniger*, mesepisternum partly to completely obscured above by white pubescence but lower part abruptly be-

coming nearly glabrous and polished with only scattered, small setae). Wings densely hairy, more so than in *T. penniger*. Metasomal terga with premarginal areas rather densely covered with fine, recumbent setae that partly obscure integument and impart somewhat grayish color to fresh specimens (in *T. penniger*, these areas with setae finer, sparser, not obscuring reddish integument); marginal areas with snowy white bands of recumbent, strongly plumose setae; anterior bands tending to be more broadly interrupted medially than posterior bands. *Premarginal areas of S3–S5 with long, plumose, white, semi-erect setae forming rather conspicuous basal bands on each sternum* (in *T. penniger*, metasomal sternal setal pattern dominated by median margin setal patch of S2 and sometimes S3, as indicated below); S2 without such a band, but with some scattered setae. *Margins of S2 and S3 medially without setae, integument polished* (in *T. penniger*, margin of S2 with conspicuous median patch of white, recumbent setae; margin of S3 often but not invariably with similar, less conspicuous patch).

Female. Structure. Head width 1.4 times length; width 1.8–2.2 mm; length 1.3–1.6 mm; wing length 4.1–4.9 mm; body length 6.1–8.0 mm.

As described for male, except for following: Eye-convergence index 0.88–0.90. Clypeal carina absent. Paraocular ridge extending only from anterior mandibular articulation to eye. Genal width 0.5–0.6 times maximum width of eye measured at right angles to posterior eye margin in lateral view. Maxillary palpus somewhat more than $\frac{1}{4}$ length of galeal blade.

Inner apex of hind tibia normal, not expanded like that of male, with two normal-sized tibial spurs.

Apex of S6 bifid, with deep median cleft.

Color. As described for male.

Integumental texture and vestiture. As described for male, except for following: Clypeus and lower paraocular areas with only scattered, recumbent, strongly plumose setae; discal area with punctures two to four puncture-widths apart (hence, clypeus as in female *T. penniger*). *Mesepisternum moderately thickly and evenly covered by suberect, pale setae* (in *T. penniger*, upper part of me-

sepisternum with dense patch of recumbent, white setae, lower part nearly glabrous as seen from side). Pseudopygidial area, like that of other Brachynomadini except for *Kelita* sensu lato, transversely oval with short setae on either side of midline directed posterolaterally; hence, each half of pseudopygidial area differentially reflective. Premarginal areas of S2–S4 with long, recumbent setae, but these setae not especially plumose, so not forming basal band on any sternum as described for male. *Margins of S2 and S3 medially without setae, glabrous* (in *T. penniger*, these sterna each bearing pronounced median patch of white, recumbent setae on margin).

HOLOTYPE: Male: MEXICO, Puebla: 14 km N.W. Izucar de Mat. [Matamoros], X-31-1991 (Rodriguez), 1220 m, salvia along road, *Protoxaea* nests; allotype, 1 km S.W. Petalcingo, XI-1-1991 (Noguera), 1280 m, old field near church in valley; 1 male paratype, same as holotype; 1 male paratype, 15 km W.N.W. Izucar de Matamoros, X-16-1986 (E. Fisher). **Guerrero:** 3 male paratypes, 13 km N.E. Taxco, X-29-1991 (T. Griswold). **Morelos:** 1 female paratype, Cuernavaca, XI-8–XII-6-1987 (F. D. Parker). These localities (fig. 42) are in a restricted area south of Mexico City.

The holotype and allotype are deposited in the Instituto de Biología, Universidad Nacional Autónoma de México, México, D.F. Paratypes are in the American Museum of Natural History and in the USDA Bee Biology and Systematics Laboratory, Utah State University, Logan, Utah.

ETYMOLOGY: From Latin: spine-bearing, referring to the highly modified apex of the male hind basitarsus (fig. 2).

HOST: Unknown.

Labels on the holotype and one male paratype state "salvia along road, *Protoxaea* nests." According to Terry Griswold (personal commun.), this information was intended as a general locality description and does not imply that these specimens were associated with a *Protoxaea* nest site or that they were necessarily associated with the plant.

PHYLOGENETIC CONSIDERATIONS

Within the Brachynomadini, *Kelita* is a distinctive element, quite different from oth-

er included genera, as was noted most recently by Michener (1996) and Rozen (1996). The discovery of *Spinokelita* with its characteristics divergent from those of *Kelita* sensu stricto suggests that *Kelita* is far more diversified than we had previously thought. As a consequence, the tribe can be considered to be divided into two lineages, the kelitine lineage (*Kelita* and *Spinokelita*) on the one hand and the brachynomadine lineage (the remainder of the Brachynomadini) on the other.

Classification in the brachynomadine lineage has been labile primarily because of the rarity of collections. Obviously, classificatory problems still persist to some extent. Such

features as numbers of submarginal cells on the forewing, numbers of segments in the maxillary palpi, and eye pubescence at this time appear to be of limited use as can now be evaluated on the basis of more specimens and a greater number of taxa. Other characters, though still used here, are suspect, such as the degree of dorsoventral compression of the body and the distance of the anterior mandibular articulation from the eye. On the other hand, characters of the male terminalia have been underutilized and show promise, as indicated in the redefinition of *Triopasites*, above. An understanding of the phylogeny of the tribe will depend on searching for reliable characters, the polarity of which can be ascertained.

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